THE BEHAVIOUR OF CAPTIVE CAPE ROCK LOBSTERS, *JASUS LALANDII* (H. MILNE EDWARDS)

By

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(With 4 figures and 15 tables)

Contents

INTRODUCTION

Various problems concerning the habits and the biology of *Jasus lalandii* have been investigated by Gilchrist (1913, 1918), Von Bonde & Marchand (1935), Von Bonde (1936), Matthews (1962), Heydorn (1965, 1966), and Lazarus (1967). However, the results of field and laboratory observations indicate that clarification of some aspects is still desirable.

It has generally been accepted that the adults moult once a year, but differences between the moulting frequencies of feral and captive animals are suggested in several reports. In certain holding experiments, Gilchrist (1913) showed that two ecdyses a year occurred in some mature females, and recent observations (Paterson, 1968; 1969a) have confirmed the prevalence of biannual ecdyses in captive animals.

There is little information regarding the mating behaviour in *J. lalandii*, and the method of insemination has been a matter of speculation. Based on the nature of the membranes of freshly-laid eggs and on the supposed absence of external spermatophores, Von Bonde (1936) concluded that fertilization probably takes place in the oviducts. This opinion has received some support from Fielder (1964c) and Heydorn (1966), but it has been noted (Paterson, 1968) that the external genital apparatus of *J. lalandii* resembles that of some Scyllaridae, in which family external spermatophores have been described by Matthews (1954a). It has also been implied (Paterson, 1968) that the mating behaviour of *J. lalandii* and the Natal rock lobster, *Palinurus gilchristi* Stebbing, may prove to be similar and that in both species the eggs are probably fertilized externally.

In pursuit of further information on the general behaviour of *J. lalandii*, various specimens were maintained at the Sea Point Aquarium from March 1966 to July 1968. During the course of the study, a soft, transparent, external spermatophoric mass was detected behind the gonopores of one experimental female. It is considered that this fact contributes towards an understanding of the process of fertilization in the Cape rock lobster.

MATERIAL AND METHODS

As soon as possible after their capture, the animals were placed in glass-fronted tanks filled with aerated sea water operating from a closed circuit. The largest experimental tank measured 72 in. × 69 in. × 48 in. and had a built-in rocky background. Frequent use was also made of ten smaller tanks, each of which was approximately 42 in. × 20 in. × 18 in. in size and had a fair depth of sand and loose stones on the bottom. In addition, a large exhibition tank, measuring 102 in. × 48 in. × 72 in. and accommodating a variable number of mature and immature rock lobsters, was also available for general observations.

From time to time, adult males and females were generously supplied by Dr. A. E. F. Heydorn, Mr. G. G. Newman and their colleagues, who collected the animals by hand during routine diving operations off Robben Island in Table Bay. Random specimens in each batch of animals were dissected to check whether the gonads were mature. In most of the experiments the sexes were paired and, as the females were generally smaller than the males, they appeared to be suitable for mating. More information concerning the habits of captive

animals was gained from 24 juvenile females, which were selected from a large number of immature animals introduced into the Aquarium in July 1966.

To avoid overcrowding, only five pairs of mature animals were placed in the largest experimental tank and usually two pairs of adults and no more than a dozen juveniles were kept in the smaller tanks. The animals were handled carefully and as seldom as possible, yet several of them lost some of their appendages at times when there was no outside interference. Most of the maimed animals were replaced by more perfect specimens, but it is probable that, had they been retained, regeneration of the injured limbs would subsequently have taken place.

The animals were maintained successfully on a daily meal of pieces of stockfish, *Merluccius capensis* Castlenau, supplemented by quantities of the mussels, *Aulacomya magellanica* (Chemnitz), various species of *Patella*, and the kelp, *Ecklonia*.

At 6 p.m. each day the electric lights in the Aquarium were regularly switched off and all the tanks were in total darkness until 9 a.m. on the following day. In an endeavour to make the conditions as normal as possible, the artificial illumination of the rock lobster tanks was dispensed with and it was found that sufficient subdued natural light reached the tanks from the outside windows of the building.

After their introduction into the tanks, the animals were inspected at least once or twice during the day, and visits of varying duration and frequency were made at night when torchlight was used for the observations. During these visits the habits of individual animals were studied.

Using steel calipers, the total cephalothoracic length (T.C.L.) was measured in millimetres from the tip of the rostrum to the postero-dorsal edge of the carapace. Heydorn (1965) has concluded that the males and females may become sexually mature when the T.C.L. is 6·0 to 6·5 cm and 7·0 cm or more respectively. In the present study few small males were handled and most of the adult females were at least 70 mm in T.C.L.

Exuviation, which usually took place at night, was seen on a number of occasions. Records of the ecdyses of individual animals were used to determine the growth rate and the length of the intermoult periods.

As few of the captive females produced eggs, attempts were made to inseminate several specimens by artificial means. In another inquiry into the possible intromission of sperm, the histology of the reproductive organs was examined. Sections were cut of part of the ovary and the entire oviduct of an ovigerous female and of portions of the testis and the vas deferens of a mature male. The sections were 10 μ thick, and alternate slides were stained with Mallory's triple stain or with Heidenhain's iron haematoxylin and eosin. Smears of seminal matrix, fixed either in osmic acid fumes or in Zenker's fluid and stained with Heidenhain's haematoxylin, were used as an additional check for possible traces of spermatophoric material in sections of the female organs.

General Observations

After becoming acclimatized to their surroundings, most of the rock lobsters established territorial rights to certain rock niches or corners in the tanks and adopted a belligerent attitude towards other animals attempting to usurp their chosen retreats. The individuals varied in their habits from day to day and, while some remained dormant for long periods, others in the same tank were often fairly active. Some degree of activity was therefore frequently observed during the day and at night in one or more of the tanks.

Most of the specimens devoted some considerable time to the diligent cleaning of the appendages or various parts of the surface of the body. The antennulary flagella seemed to receive most attention, being repeatedly drawn through the apposed medial setose margins of the third maxillipeds. The latter were then rubbed together and apparently cleaned after the antennulary flagella had been released.

Occasionally some of the legs of one side were hooked over and drawn as far as possible along the antennal flagellum of the same side, the surface of which was presumably brushed by the spines and setae on the dactyls. The antennal peduncles, the eyes, and parts of the cephalothorax were most frequently cleaned by the dactyls of the second or the fourth pereiopods.

In both sexes the dactyls of the fifth legs were employed to scrape the surfaces of the abdomen and the pleopods. As remarked by Gilchrist (1913), Von Bonde & Marchand (1935), Von Bonde (1936), and Fielder (1964b), ovigerous females habitually used the chelae of the fifth legs to groom the incubation chamber. The loosened debris was probably cleared by the subsequent vigorous flapping of the pleopods, which at times was also instrumental in releasing swarms of larvae.

When not engaged in grooming, many of the animals rested on the bottom of the tanks, usually supported by the flexed tail-fan and the posterior legs, while the other legs swayed leisurely to and fro. Such limb movements appeared to be rather aimless, but they were doubtless of consequence in maintaining the stream of respiratory water entering the branchial chambers at the bases of the legs.

Occasionally some individuals were observed drawing the anterior legs through the sand, and several specimens seemed to be fastidious about their resting-places. Some of the occupants of the smaller tanks dug pits in the sand in which they later rested. Fairly heavy loose stones lying in front of the bottom rock recesses in the large tank were often forcibly removed, probably to make the retreats more accessible.

Locomotor and Feeding Activities

From June to September 1966, a study was made of the locomotor and feeding activities of ten pairs of adult rock lobsters which had been in captivity for two months before the observations began. The T.C.L. of the animals
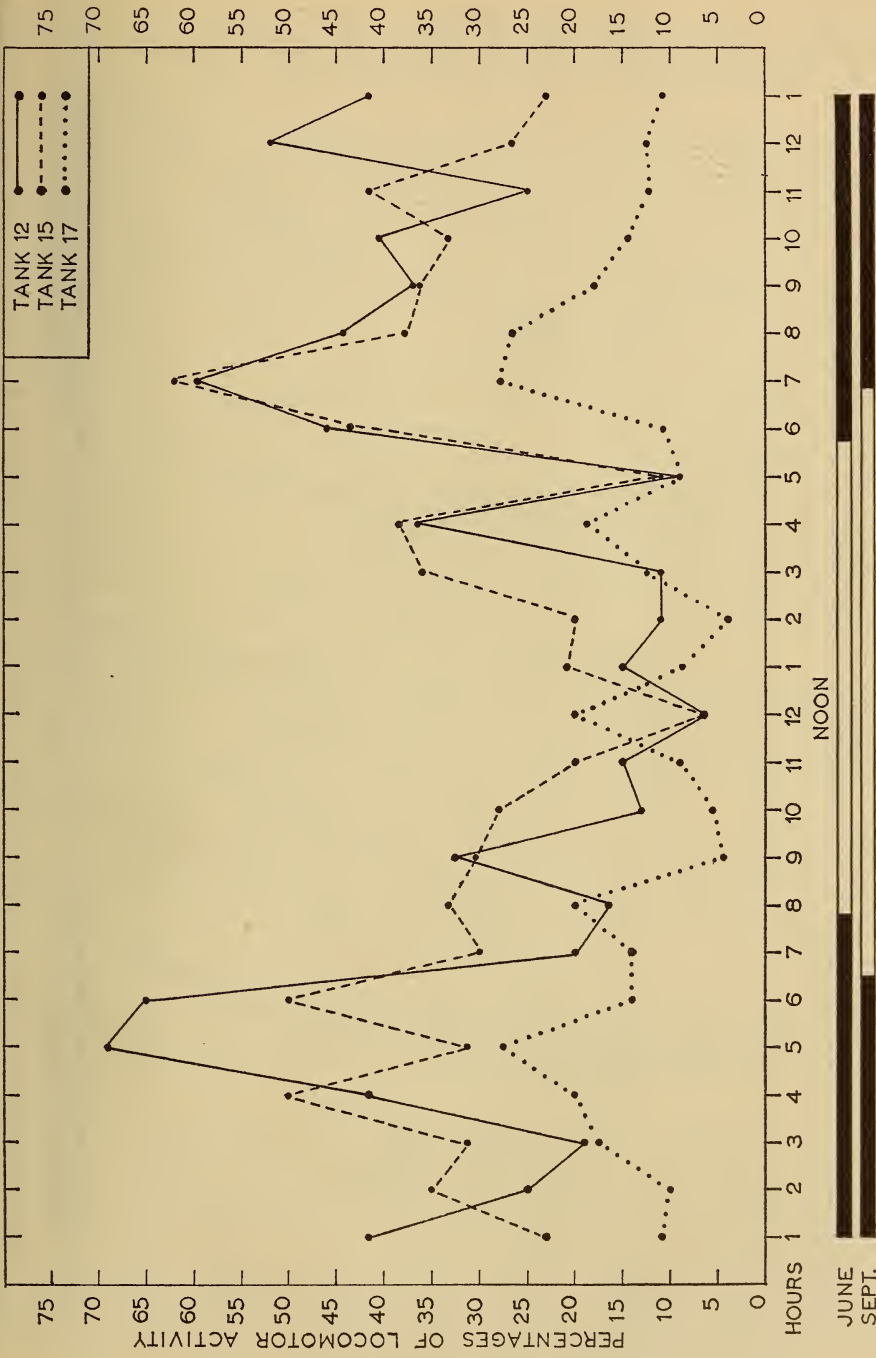
FIG. 1. The hourly variations in the locomotor activity of three groups of adult rock lobsters for the period 1 June to 30 September 1966. Tanks 12 and 15 measured about 42 in. × 20 in. × 18 in. and each contained two pairs of animals. Tank 17 measured 72 in. × 69 in. × 48 in. and contained five pairs of animals. Food was supplied regularly each day between 3 and 4 p.m. The hourly counts of active animals are expressed as percentages of the number of animals present. The black bands represent the average hours of darkness in June and September.
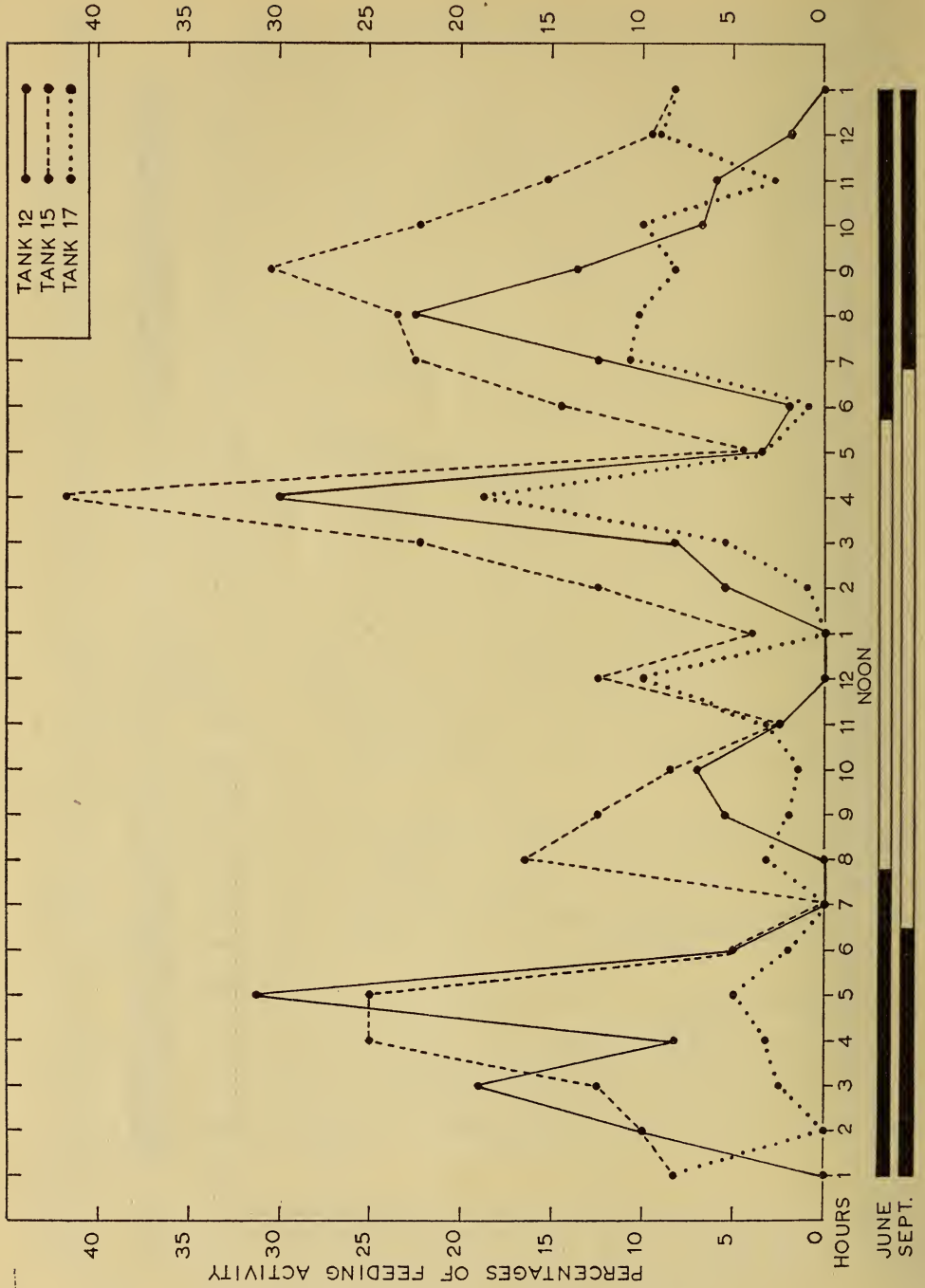
Fig. 2. The hourly variations in the feeding activity of the same animals and for the same period as in figure 1. The hourly counts are also expressed as percentages of the number of animals present. A high level of activity was evident during the afternoon when food was introduced into the tanks.

ranged from 78 to 122 mm in the males and from 83 to 100 mm in the females. Exploratory movements away from an established niche were regarded as locomotor activity, while actual seizure and consumption of food were recorded as feeding activity.

Intermittent observations of the tanks were made at least twice an hour during the day and at night, and the hourly counts of the animals active were expressed as percentages of the total number of animals present. These percentages were used to determine the mean hourly variations in the locomotor and the feeding behaviour during the four months in question (figs 1, 2).

From the above figures a comparison may be made between the hourly activities of 18 animals located in two of the smaller tanks (nos 12, 15) and the larger experimental tank (no. 17). The results suggest that the four animals in each of the two smaller tanks were generally more active than the ten animals in the larger tank. Although the animals in the smaller tanks were by no means cramped, they probably disturbed one another more frequently than did the animals in the larger tank, in which some specimens remained quiescent in their rock shelters for relatively long periods.

The graphs shown in figures 1 and 2 may also be used to illustrate the hourly levels of activity over a period of four months. Three main peaks of locomotor and feeding activity are indicated, one occurring before sunrise, another between 3 and 4 p.m., and a third after sunset.

The normal rhythms of foraging and feeding were doubtless disturbed by the daily introduction of fish into the tanks between 3 and 4 p.m. Consequently, the marked afternoon increase in activity appears to be anomalous. If, however, the responses to artificial feeding are excluded, a bimodal rhythm seems to be suggested in both the locomotor and the feeding activity.

A somewhat similar bimodal cycle has been reported by Kubo & Masuda (1964) in the feeding habits of captive specimens of *Panulirus japonicus*. It was established that the twilight peaks roughly corresponded with those found in fishing experiments, but the dawn peak of the latter was two hours later than the corresponding peak in the captive animals.

On the other hand, in captive *Jasus novaehollandiae* (*lalandii*), Fielder (1965) observed that the maxima for both the locomotor and the feeding activity occurred at dusk. This may imply that the normal rhythm is unimodal in this species.

Following procedures suggested by Sutcliffe's (1956) experiments on captive *Panulirus argus*, the hourly counts of activity in 18 to 20 animals formed the basis of a comparison between the day and the night locomotor and feeding activities (table 1). The observations covered the same period of four months indicated in figures 1 and 2, but, in addition to the previously mentioned 18 animals, another pair was maintained in a separate tank during June and July. The means are represented as percentages of the quotients of the total number of animals present and the number of active animals observed in hourly counts throughout the whole period.

TABLE 1

Summary of counts of the diurnal and the nocturnal locomotor and feeding activities of 18 to 20 adult rock lobsters for the period June to September 1966. The means are expressed as percentages of the total number of animals present.

Time	No. of hourly counts	No. of animals present	No. of animals foraging	Mean % of locomotor activity	No. of animals feeding	Mean % of feeding activity
Day	149	2850	414	14·5	194	6·8
Night	194	3748	1093	29·2	423	11·3

Applying Hoel's (1962) formula for testing the difference between two proportions to the data in table 1, an assessment was made of the respective day and night proportions of activity relative to the number of animals present.

The values of z were 14·1 and 6·2 with regard to the locomotor and feeding activities respectively. This means that in both foraging and feeding the difference between the day and the night activity was significant at the 1 % level.

It has been concluded that, although the daily introduction of food during the afternoon affected the diurnal counts, there was an increase in both types of activity at night.

ECDYSIS

Most of the animals were soft to the touch about two weeks before ecdysis, but in a few large males proecdysis apparently began nearly three weeks before the animals moulted. During this time the animals tended to become gradually more quiescent, but they had occasional periods of restiveness. Feeding was usually suspended for approximately five to seven days before ecdysis and was resumed in four to eight days after the event.

As has been indicated in *Panulirus* by Travis (1954) and other investigators, the first obvious sign of proecdysis was the appearance of a resorptive line running somewhat obliquely backward and downward along the branchiostegite to its posterior articulation with a condyle on the last thoracic epimeron. This line is probably more noticeable in species of *Panulirus* than in *J. lalandii*, in both sexes of which a longitudinal pale streak is commonly present on the branchiostegite more or less in the position of the suture along which calcium resorption takes place during proecdysis.

About four to seven days before ecdysis the resorptive line was most clearly seen by torchlight at night. It resembled a shining, greasy-looking marking along each branchiostegite with an additional, short, broad band extending downward at the junction of the branchial and the prebranchial chambers. Even though the resorptive line became progressively more marked, it was less

obvious in the adult males than in mature females, but was very distinct in both sexes of juvenile animals.

As the time for exuviation approached, the animals usually became very restless and the body had a somewhat deformed appearance owing to an apparent loosening of the parts at the junction of the thorax and the abdomen. This was often evident about 24 hours before ecdysis and was associated with the gradual exposure of the first abdominal tergum and a widening of the gap between the carapace and the flange on the first abdominal segment. The abdomen was then frequently held in the fully extended position, but the animals were still able to move about fairly rapidly, although rather clumsily.

About two to three hours before exuviation in the juveniles and 45 to 75 minutes in the adults, the animals seemed to be more perturbed and were noticeably hostile towards other rock lobsters in the tank. As they roamed about, the antennae were held aloft and the pleopods, which were often pendent at this stage, were swung leisurely to and fro. During short periods of rest, the antennulary flagella were drawn vigorously through the apposed margins of the third maxillipeds. The pereiopods and even the eyes were moved restlessly in various directions, and at intervals the first abdominal segment was thrust forward below the posterior margin of the carapace. Travis (1954) has suggested that similar activities in *Panulirus argus* probably help to loosen the old exoskeleton from the underlying new one.

Immediately before ecdysis began, the animal became more agitated and attempted to brace itself on the bottom of the tank or over a loose stone, occasionally exhibiting convulsive movements. If, as frequently occurred, it happened to be disturbed by other individuals at this juncture, it was still able to evade them by darting swiftly backward through the water.

As in other species, the movements in *J. lalandii* were accompanied by the gradual and extraordinary swelling of the thoraco-abdominal intertergal membrane which, according to Drach (1939) and subsequent observers, is effected by water absorption and increased pressure in the pericardial pouches.

The distension of the membrane seemed to be less rapid in the juveniles than in the adults. In the former the membrane began to stretch at least 80 minutes before ecdysis, while in the adults it was usually first visible about 30 to 40 minutes before actual exuviation. When the dorsal membrane became markedly stretched, the animal seemed to be less sensitive to light. It settled down fully extended, supported on the tips of the pereiopods and the edge of the tail-fan and often with the antennae directed forward.

The preliminary step of exuviation was the detachment of the lower margin of the old branchiostegite from the new exoskeleton, as a result of which the posterior border of the old carapace was slightly raised. Thereafter, the dorsal intersegmental membrane became progressively more taut until eventually the posterior edge of the new carapace was clearly visible through the membrane. At the same time, the bracing action of the limbs and the somewhat telescopic movements of the abdominal segments probably created additional

pressure required for the implementation of ecdysis.

Rupture of the fully stretched membrane was sudden, and the old carapace began to rise quickly and almost imperceptibly until it was tilted forward at an angle of about 90 degrees. After the eyes had been withdrawn, the animal seemed to find purchase against the anterior and lower parts of the old exoskeleton while the antennae, the legs, and the successive abdominal segments were freed from their previous casings. Almost simultaneously, the sternum and the old endoskeleton were released and, with a sudden convulsive movement, the animal extricated itself from its former skeleton.

Most of the young rock lobsters were inclined to dart out from the right side of the exuviae, but in the adults the procedure seemed to be more normal and they emerged dorsally through the wide gap between the raised carapace and the first abdominal tergum of the old exoskeleton. Once the animal had moulted, it appeared to be unusually excited and very sensitive to light, and its rather flexible antennal flagella were swept through the water with considerable force.

Ecdysis usually took place at night, but was also recorded before noon in two adult males and one female. The exact time of ecdysis was somewhat variable, and in observations of 11 juveniles and seven adults (fig. 3) it ranged from 22 minutes before sunset in the largest specimen to over six hours after sunset in one immature female.

In both the juveniles and the adults exuviation was generally completed in three to five minutes and there appeared to be no direct correlation between the size of the animal and the duration of ecdysis. Nor did the time of the year have any obvious effect on the period required for emergence. Eight of the observations below were made in spring, six in summer, two in autumn, and two in winter. It may also be remarked that one of the summer ecdyses was that of a female (T.C.L. 77 mm) which had produced eggs in captivity 140 days before this particular ecdysis.

The mean duration of exuviation in the 18 animals was $4 \cdot 4 \pm 0 \cdot 95$ minutes. This average includes the exceptional time of seven minutes recorded in one immature animal (T.C.L. 58 mm) which required short periods of rest between frenzied efforts to free its legs. During the struggle, the old exoskeleton was torn asunder, and in several unsuccessful ecdyses of adult animals the exuviae were found to be similarly dismembered.

The main difference between ecdysis in *J. lalandii* and the process described in other Decapoda is in the time taken for the withdrawal of the animals from their exuviae. Drach (1939) observed that the period required in Brachyura was 10 to 30 minutes, while in *Panulirus* it seems to vary with the species. Several accounts show that it is about 15 minutes in *P. japonicus* (Nakamura, 1940), three to five minutes in small specimens and five to ten minutes in somewhat larger individuals of *P. argus* (Travis, 1954), 11 to 18 minutes in *P. interruptus* (Lindberg, 1955), and eight to ten minutes in *P. cygnus* (Thomas, 1966). In figure 3 it is evident that the normal duration of ecdysis in the
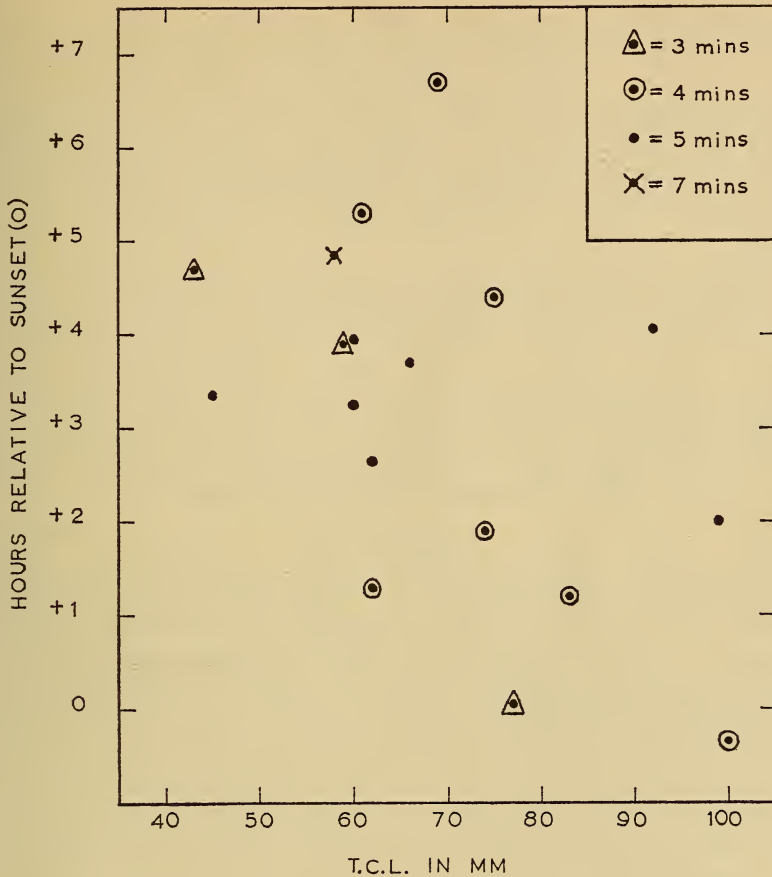
FIG. 3. Starting times of ecdysis in 18 animals, plotted to the nearest minute before or after sunset (o). The duration of ecdysis is indicated by the symbols shown in the key. The T.C.L. of the individuals ranged from 43 to 100 mm.

juveniles of *J. lalandii* is comparable to that observed by Travis (1954) in young forms of *P. argus*, but in the adults it is shorter than in other palinurids.

During 1967 some records were also kept of ecdysis in a number of males of *J. tristani* exhibited at the Sea Point Aquarium. The exuviation of three specimens with cephalothoracic measurements of 83 mm, 105 mm, and 119 mm occurred about two hours after sunset and took four minutes, five minutes, and seven minutes respectively. The process was similar to that of *J. lalandii*, except that before and during ecdysis the animals were more composed than moulting specimens of the local species and withdrawal from the exuviae was effected with a minimum of effort. Such deliberate action was, however, consistent with the habits of these fairly large rock lobsters which were generally more placid than the captive juveniles and adults of *J. lalandii*.

Several investigators have stated that during ecdysis in palinurids the old exoskeleton fractures along the resorptive lines but, as in *Panulirus argus* (Travis, 1954), this does not eventuate in *J. lalandii* or in *J. tristani*. The sutures along the branchiostegites are softened by calcium resorption and, although they are easily broken while handling the exuviae, they normally remain intact and simply serve as pliable seams along which the side flaps of the otherwise rigid exoskeleton are able to bend slightly when the carapace is raised during ecdysis.

From an examination of exuviae, it is further evident that the carapace becomes detached from the thoracic epimeral plates and that it is hinged at the base of the epistoma. As Drach (1939, 1950) has shown in his comprehensive studies of ecdysis, withdrawal of the animal is also facilitated by extensive resorption of the medial elements of the endoskeleton. The resultant gaps in the old endoskeleton are not only essential for the speedy release of the sternum and the thoracic appendages, but their presence also accounts for the obvious weakness of animals in the so-called 'soft old shell' stage.

All newly shed exuviae are provided with a thin slimy lining which, according to Drach (1939) and Passano (1960), is formed during proecdysis from a membranous layer adjacent to the epidermis. As these authors have suggested that this lining may serve as a lubricant for the easy withdrawal of the animal, it seems likely that a deficiency of mucilage may be one of the causes of death during ecdysis. Failure to extricate the appendages and the exposure of some of the gills and epipodites appeared to be common reasons for fatalities during or shortly after ecdysis in some of the present animals.

In most of the captive animals the new integument seemed to be fairly hard about three weeks after ecdysis, but the time required under natural conditions is not known. Drach (1939) has shown that some of the calcium necessary for the reconstruction of the new exoskeleton is derived from food intake and from reserves in the digestive gland (hepatopancreas). He has also concluded that calcium absorption from the sea water, particularly during the first stages of the moulting cycle, is of great importance in the consolidation of the new exoskeleton. A calcium deficiency in the external medium would therefore be detrimental to postecdysial animals in that hardening of the exoskeleton would be retarded. Chemical tests of the water in the rock lobster tanks indicated, however, that the calcium level was satisfactory.

REGENERATION OF THE APPENDAGES

Renewal of appendages, which had been lost either before or shortly after the animals were captured, also accompanied ecdysis in some adult and juvenile specimens. The amputation of an injured pereiopod invariably took place at the fracture plane between the basipodite and the ischiopodite, and the extremity of the stump was then sealed by an obvious black scab.

At the next ecdysis, all the segments of the limb had been reformed, but

they were always shorter and thinner than normal. Dissections of several animals which died during exuviation showed that the soft regenerating limbs were neatly folded within the stumps of the old limbs.

Occasionally an antennal flagellum, which had fractured close to the peduncle, was partly regenerated during one intermoult period, but usually it was no more than half its normal length. In one specimen, in which the antenna had apparently been severely injured, a short bifurcated antennal flagellum was produced when the animal moulted. In another specimen, which had lost the right middle pereiopod and the left antennal flagellum, two ecdyses were required before the limb had regained its natural proportions and strength. The left antennal flagellum, however, only became subequal to the one on the other side after three ecdyses.

This fairly rapid replacement of injured appendages in *J. lalandii* is compatible with Bradstock's (1950) observations of autotomy and autospasy of the pereiopods and autospasy of the antennae of *J. edwardsii* (*lalandii*), in which an antennal flagellum became fully regenerated within a year.

CANNIBALISM

From time to time cannibalism of recently-moulted juveniles occurred in the large exhibition tank. It was common when the animals were somewhat crowded and a greater competition for food was likely.

In one instance, a young, newly-moulted female (T.C.L. 52 mm) was relentlessly attacked by two other rock lobsters of a similar size and died within half an hour. One assailant immediately tore out the eyes and at the same time presumably destroyed the brain, while the second cannibal confined its attention to the posterior end of the body. This observation is of interest inasmuch as Carlisle (1953) has reported that prawns kept under crowded conditions devour the eyestalks of dead specimens before eating other parts of the body.

Cannibalism was not observed among immature and adult experimental animals which were less confined and probably better nourished than the other captive rock lobsters. In some of the tanks, however, the exuviae were occasionally partly eaten before they could be removed.

From all accounts, the consumption of exuviae is usual in Crustacea and is not confined to captive animals. Its occurrence in the latter may indicate an inadequate supply of their natural food which could lead to cannibalism in hungry animals and result in a reduction of the stock. Drach (1939) has indicated that certain species eat exuviae as a source of calcium for accelerating the hardening of the exoskeleton after ecdysis. He has, however, also remarked that some animals will consume exuviae, not because of a need for calcium, but because no other food is available.

AVERAGE RATE OF GROWTH

The exoskeleton was allowed to harden for about three weeks before the average growth rate was determined by comparing the premoult and the

postmoult cephalothoracic measurements of individual specimens. The moult increments in T.C.L. for the juvenile females, the adult males, and the adult females are considered separately in tables 2 to 4.

TABLE 2

Average growth rate per moult in juvenile females

T.C.L. in mm	No. of specimens	Increase in mm	Mean increase in mm	Mean % increase
20–29	3	2·25–2·5	2·4	8·8
30–39	4	2·5–3·0	2·6	7·5
40–49	3	2·5–3·0	2·8	6·5
50–59	12	0·0–4·0	2·5	4·4
60–69	9	0·0–4·25	2·8	4·4

TABLE 3

Average growth rate per moult in adult males. No specimens with a T.C.L. of 80 to 89 mm were available

T.C.L. in mm	No. of specimens	Increase in mm	Mean increase in mm	Mean % increase
70–79	7	1·5–3·0	2·4	3·1
90–99	9	2·0–3·0	2·4	2·6
100–109	8	1·0–3·5	2·3	2·2
110–119	3	2·0–3·0	2·3	2·0

TABLE 4

Average growth rate per moult in adult females

T.C.L. in mm	No. of specimens	Increase in mm	Mean increase in mm	Mean % increase
70–79	9	0–2·0	1·8	2·4
80–89	20	0–3·0	2·1	2·5
90–99	8	0–3·0	2·1	2·2
100–109	3	0–3·0	1·7	1·7

An examination of the above percentage increases in length in the various size classes shows that the growth rate decreases as the animals become larger. A somewhat similar gradation in the growth rate of a greater number of specimens of *J. novaehollandiae* has been reported by Fielder (1964a).

The increase in the T.C.L. of the adults was usually 2·0 or 3·0 mm at each ecdysis, but in some individuals the increments fluctuated at successive ecdyses and occasionally little or no difference in size was noted. In a few of the adults the growth of the body was probably moderated by the necessary regeneration of one or more injured appendages, but relatively low values were also common in a number of perfect specimens.

Although there is no relationship between the T.C.L. and the growth increments in the present small samples, an attempt was made to examine the difference between the mean increments of the adult males and females on the one hand and the adult females and the juvenile females on the other hand. The relevant statistics are summarized in table 5.

TABLE 5

Estimated mean increases in T.C.L. per moult in captive animals, together with the standard deviations and the *t* values

	No. of specimens	Mean increase in mm	Standard deviations	t values	
Adult males	27	2·37	·64	1·83	
Adult females	40	2·02	·86		2·50
Juvenile females	31	2·62	1·07		

From the statistical information in table 5, it has been calculated that:

1. In the ratio of the adult males to the adult females, with 65 degrees of freedom, a *t* value of 1·83 is significant at the 10% level only. Thus, no appreciable difference in the growth increments of the captive adult males and females was apparent.

2. In the comparison between the adult females and the juvenile females, with 69 degrees of freedom, a *t* value of 2·5 is significant at the 5% level. It is therefore probable that the T.C.L. moult increments of the juvenile females slightly exceeded those of the adult females.

It may be remarked that the increments shown in tables 3 and 4 are lower than those in Heydorn's (1966) field observations, in which the natural growth rate of 19 tagged adults of *J. lalandii* ranged from 2·0 to 8·5 mm per moult. None of the present experimental adults increased by more than 3·5 mm in T.C.L. after any one ecdysis, and a diminution of the growth rate was evident at the consecutive ecdyses of several animals. Some confirmation of Lindberg's (1955) suggestion that growth is probably retarded in captive animals may

therefore be indicated.

At the same time, some of the length increments recorded by Heydorn (1966) appear to be greater than would be expected at a single ecdysis. His results are obviously based on the conclusion that there is an annual ecdysis in the adults of *J. lalandii*, but it was found that biannual ecdyses were common in the present captive animals. If it should later be established that there is more than one ecdysis a year in the field, it is probable that the average growth rates of captive and free-living rock lobsters may prove to be more compatible than is at present apparent.

INTERMOULT PERIODS

From May 1966 to July 1968, 109 ecdyses (table 6) were recorded at different times of the year in 75 adults, comprising 28 males (T.C.L. 71 to 122 mm) and 47 females (T.C.L. 66 to 102 mm). During much the same period, 38 ecdyses (table 6) occurred in 18 immature females (T.C.L. 26 to 69 mm).

TABLE 6

Summary of the number of seasonal ecdyses in captive rock lobsters
from May 1966 to July 1968

Specimens	Autumn	Winter	Spring	Summer
Adult males	4	8	17	10
Adult females	12	17	18	23
Immature females	8	7	15	8

Of the 75 adults, 18 males and 29 females either died or were abandoned after their first ecdysis. Thirteen of the 29 females, including one with a T.C.L. of 66 mm, had been collected in berry during the winter breeding season, and all of them moulted the following spring or summer after the eggs had hatched.

As indicated in a brief account of the ecdyses of captive rock lobsters (Paterson, 1969a), the remaining 28 adults were maintained for a year or longer (table 7) and usually moulted in autumn or winter and again in spring or summer.

TABLE 7

Summary of the plural ecdyses in individual adult
rock lobsters from May 1966 to July 1968

	Four ecdyses in 24 months	Three ecdyses in 18 months	Two ecdyses in 12 months
Males	0	1	9
Females	1	3	14

Most of the females which survived two or more ecdyses failed to spawn, but three of them moulted in captivity before producing eggs and each had a second ecdysis five or six months later.

In 26 of the 28 animals enumerated in table 7 definite spring/summer to autumn/winter and autumn/winter to spring/summer intermoult periods occurred (tables 8, 9). The two exceptional animals were females, in one of which (T.C.L. 72 mm) there was a short spring to summer intermoult period of 119 days and in the other (T.C.L. 85 mm) a winter to early spring intermoult period of 105 days. These two intermoult periods have been omitted in tables 8 and 9.

TABLE 8

Duration of the spring/summer to autumn/winter intermoult period in adult males and females

T.C.L. in mm	No. of intermoult periods		Intermoult periods in days		Mean duration of intermoult periods in days
	Males	Females	Males	Females	
70–79	1	1	154	201	177·5
80–89	0	4	0	176–220	191·2
90–99	1	1	147	213	180·0
100–109	1	0	207	0	

TABLE 9

Duration of the autumn/winter to spring/summer intermoult period in adult males and females

T.C.L. in mm	No. of intermoult periods		Intermoult periods in days		Mean duration of intermoult periods in days
	Males	Females	Males	Females	
70–79	0	3	0	120–185	148·3
80–89	0	6	0	143–188	158·3
90–99	3	4	166–198	146–166	164·1
100–109	4	2	161–186	150, 188	171·6
110–119	1	0	173	0	

Although the number of examples is small, it seems obvious that in the adults the interval between the spring/summer and the autumn/winter ecdyses is the longer of the two intermoult periods.

Ecdysis was irregular in the immature females, but some correlation

between the size of the animals and the length of the intermoult periods is indicated in table 10.

TABLE 10

Intermoult periods in the various size classes of juvenile females

T.C.L. in mm	No. of intermoult periods	Intermoult periods in days	Mean duration of intermoult periods in days
20–29	2	72, 81	76·5
30–39	3	71–107	87·7
40–49	2	85, 102	93·5
50–59	8	87–223	157·8
60–69	4	152–234	185·2

In the 50 to 59 mm size class short periods of 87, 120, and 127 days were referable to three animals measuring 53 to 57 mm in T.C.L. The other animals in this and in the 60 to 69 mm size class underwent two ecdyses a year, one in spring or summer and the other in autumn or winter. Two distinct intermoult periods were thus recognized in several animals (tables 11, 12).

TABLE 11

Duration of the spring/summer to autumn/winter intermoult period in juvenile females

T.C.L. in mm	No. of specimens	Intermoult periods in days	Mean duration of intermoult periods in days
50–59	3	203–223	211·7
60–69	3	152–234	195·3

TABLE 12

Duration of the autumn/winter to spring/summer intermoult period in juvenile females

T.C.L. in mm	No. of specimens	Intermoult periods in days	Mean duration of intermoult periods in days
50–59	2	141, 151	146
60–69	1	155	

As in the adults, there is a difference between the mean duration of the two intermoult periods in the juvenile females, but too few specimens were handled for a true assessment to be made of the length of either period. In agreement with Fielder's (1964a) observations on *J. novaehollandiae*, however, a progressive lengthening of the intermoult period is indicated (table 10) as the animals increase in size. Fielder (1964a) has also ascertained that in 33 *J. novaehollandiae*, measuring from 5·0 to 5·9 cm in T.C.L., the average intermoult period was 137 days from July to December and 158 days from January to June.

MOULTING FREQUENCIES AND ANNUAL RATE OF GROWTH

No observations were made of the behaviour of captive immature male rock lobsters, but some information was gained regarding the consecutive ecdyses of several juvenile females and adult males and females.

Although the records are somewhat meagre, a tentative estimate of the mean annual frequency of moulting may be obtained from a consideration of the duration of the intermoult periods in the various size classes (tables 13, 14). In addition, the probable annual increase in T.C.L. has been appended to each size class in tables 13 and 14.

In collating the data, the two short intermoult periods of 119 and 105 days, which were omitted in tables 8 and 9, have been included in table 13 in the mean intermoult periods of the 70 to 79 mm and 80 to 89 mm size classes respectively.

TABLE 13

Mean frequency of moulting and annual increase in T.C.L. in captive female rock lobsters

T.C.L. in mm	No. of specimens	Mean intermoult in days	Mean frequency of moulting per annum	Mean increase per moult in mm	Annual increase in T.C.L. in mm
20–29	2	76·5	4·8	2·4	11·5
30–39	3	87·7	4·2	2·6	10·9
40–49	2	93·5	3·9	2·8	10·9
50–59	8	157·8	2·3	2·5	5·8
60–69	4	185·2	2·0	2·8	5·6
70–79	5	153·0	2·4	1·8	4·3
80–89	11	165·5	2·2	2·1	4·6
90–99	5	164·8	2·2	2·1	4·6
100–109	2	169·0	2·2	1·7	3·7

TABLE 14

Mean frequency of moulting and annual increase in T.C.L. in captive adult male rock lobsters.
No specimens were available in the 80–89 mm size class

T.C.L. in mm	No. of specimens	Mean intermoult in days	Mean frequency of moulting per annum	Mean increase per moult in mm	Annual increase in T.C.L. in mm
70–79	1	154·0	2·4	2·4	5·8
90–99	4	171·2	2·1	2·4	5·0
100–109	5	179·8	2·0	2·3	4·6
110–119	1	173·0	2·1	2·3	4·8

The moulting frequencies seem to be rather variable, but it may be concluded that, as the animals increase in size, they undergo fewer ecdyses a year. It is also apparent that there is a corresponding diminution in the annual growth rate.

The above results indicate that the smallest rock lobsters may moult at least four times a year and that, correlated with the lengthening of the intermoult periods in the larger size classes, the number of ecdyses is reduced to three and then to two a year.

Two or more ecdyses a year occurred in only ten of the experimental juvenile females, and direct observations suggest that the transition from three to two annual ecdyses may take place in animals with T.C.L. measurements of 53 to 57 mm. The occurrence of biannual ecdyses in the 60 to 69 mm size class is of interest and may denote that the moulting rhythm of young animals approaching puberty is similar to that of the adults.

A higher moulting frequency in immature than in mature specimens of *Jasus* has been reported by Hickman (1945) and Bradstock (1950). More recently, Fielder (1964a) has found that in *J. novaehollandiae* the average number of annual ecdyses is three in specimens with a rostrum-carapace length of 5·0 to 7·9 cm and two in the 8·0 to 8·9 cm size class.

As shown in table 7, two ecdyses a year took place in 28 adults which survived their first ecdysis in captivity. It may also be remarked that, in the few animals which moulted more than twice, the cyclical sequence (Paterson, 1969a) was sufficiently regular to warrant the conclusion that a definite and recurrent moulting rhythm is established in individual rock lobsters.

It was suggested by Gilchrist (1913) that the adults of *J. lalandii* probably moult once a year, the males in spring (September and October) and the females in mid-winter. In four captive females, however, he observed that two of them moulted annually, while two ecdyses a year occurred in the other two animals. Except for the omission of the annual dates, the table and comments published by Von Bonde & Marchand (1935) are similar to Gilchrist's (1913)

findings and provide no further information as to the frequency of ecdysis in mature females.

More recent observations by Matthews (1962) and Heydorn (1965) on populations of adult rock lobsters off the west coast of South Africa have not determined that there is more than one ecdysis a year. From his investigations on the biology of *J. lalandii* found off Robben Island, Heydorn (1966) has concluded that most of the adult females moult in late autumn or early winter (May and June) before mating begins and that there is a marked increase in the ecdysis of adult males during late spring and summer (November to February).

It has also been inferred by Heydorn (1966) that captive 'unfertilized females undergo an untimely moult four or five months after the normal annual moult'. Nevertheless, biannual ecdyses were indicated in both sexes of the present captive animals (tables 7–9), and a spring/summer ecdysis took place, not only in unmated females, but also in females which had previously been in berry.

Investigations by Crawford & De Smidt (1922), Nakamura (1940), Sutcliffe (1953), Lindberg (1955), George (1962), and Sheard (1949, 1962) have also proved that the mature females of various species of *Panulirus* undergo two ecdyses a year, one before mating and the other after the eggs have hatched. It is even more pertinent to the present study that Grua (1964) has reported the occurrence of winter and summer ecdyses in the females of *Jasus paulensis*.

Ovigerous Setae

After it was found that the captive adults moulted twice a year, more attention was paid to the condition of the ovigerous setae. During a period of two years, 70 observations were made of the setal arrangement at the successive ecdyses of 33 females which either possessed ovigerous setae when they were collected or acquired them at their first ecdysis in captivity.

If, as is detailed in the appendix, the presence and absence of the ovigerous setae are respectively represented by plus and minus signs, the following definition of the setal history relative to the biannual ecdyses is obtained:

Autumn/winter ecdyses: $+ = 31$; $- = 5$
Spring/summer ecdyses: $+ = 3$; $- = 31$

In an analysis of 37 pairs of ecdyses referable to the 33 females (see appendix), the sequence of setal $(+)$ and a-setal $(-)$ ecdyses was found to be:

$(+, -) = 30$; $(+, +) = 2$; $(-, +) = 1$; $(-, -) = 4$

The above summaries show that, whereas 31 of the females possessed ovigerous setae at the autumn/winter ecdysis, only three females produced setae at the spring/summer ecdysis. It is also apparent that in most of the females there was an almost regular biannual development and loss of the ovigerous setae.

There is no doubt that the ovigerous setae are acquired when the females attain sexual maturity. Consequently, if the alternation of the setal and the a-setal phases observed in captive females is normal, it suggests that in a large population of rock lobsters there may sometimes be a number of mature females which lack ovigerous setae. Such females could be described as being in a state of sexual rest and would resemble immature animals if the setae had been shed at an ecdysis following the incubation of the eggs.

Little is known about this aspect of *J. lalandii* in the field, but Bradstock (1950) has concluded that a relatively high percentage of the females of *J. edwardsii* retain the ovigerous setae after the eggs have hatched. In *Panulirus*, on the other hand, accounts by Nakamura (1940), Sutcliffe (1953), and George (1962) indicate that the females moult and shed the ovigerous setae after the breeding season.

In *J. lalandii* large ovaries containing brick-red or orange eggs are typical of females possessing long ovigerous setae. It was therefore of interest that apparently mature ovaries were observed in three unmated females after a lengthy period of captivity and upon renewal of the ovigerous setae at the winter ecdysis. By contrast, in a number of unmated and post-ovigerous females, which lost the ovigerous setae at the spring/summer ecdysis, the ovaries were narrow and only slightly folded and the eggs were small and white.

Apart from some observations by George (1958) and Fielder (1964b), the correlation between the condition of the ovaries and the setal arrangement in the Palinuridae seems to have been hardly investigated. The significant results of experiments performed by Charniaux-Cotton (1960) on *Orchestia gammarellus* may, however, be mentioned in this connexion. In this amphipod it has been shown that the oostegites revert to the juvenile state and have shorter ovigerous setae when the ovaries are inactive. It has been concluded that the ovigerous setae of *Orchestia* are temporary sexual characters associated with the incubation of the eggs and that their growth is induced by an ovarian hormone which is secreted during vitellogenesis.

It seems reasonable to suppose that similar conditions may prevail in some palinurids and that the absence of ovigerous setae is connected with the immature state of the eggs between one reproductive cycle and the next. At such a time, hormonal control of the external secondary sexual characters would be precluded and, if an ecdysis ensues shortly after the eggs have hatched, it is unlikely that ovigerous setae will be formed at this ecdysis. It thus appears that, even though the moulting frequencies of experimental animals suggest that the mature females of *J. lalandii* may moult twice a year, only one incubatory period will be possible if the ovigerous setae are shed at one or the other of the two ecdyses.

Grua (1964) has concluded that the damaged setae of post-ovigerous females of *Jasus paulensis* are replaced at a summer ecdysis which is quite distinct from the one that precedes mating. The present observations indicate, however, that in most captive *J. lalandii* females the ovigerous setae are renewed

only at the premating ecdysis. There is also a strong probability that the latter takes place in late autumn or winter in some females (31 in the present study) and in spring in other females (3 in the present study).

If this opinion is correct, it may explain why one of the captive females in Gilchrist's (1913) experiments spawned on two different occasions after the second ecdysis, while another female spawned after the first ecdysis. As the moulting cycles of these two females are more or less comparable with the present findings, it is surmised that the ovigerous setae were developed at the second ecdysis in Gilchrist's first female and at the first ecdysis in the second female.

Although most of the females of *J. lalandii* are apparently equipped for carrying eggs after the autumn/winter ecdysis, it has been shown that a considerable number of the captive females discarded their ovigerous setae at the spring/summer ecdysis. It may be noted, however, that two females, which were captured in berry towards the end of winter, did not moult until the following autumn and the ovigerous setae were again renewed and not lost. As these females were included in an independent tagging experiment, they have been omitted from the above considerations. Nevertheless, if their behaviour was normal, it introduces the possibility that in some females the post-incubatory ecdysis may be omitted and that the premating ecdysis may occur at slightly different times in consecutive years.

REPRODUCTION

Most of the mature females were provided with apparently suitable partners, but mating was not observed and only five females produced eggs. Two of the females were soft when collected and, as they became ovigerous in 11 and 18 days after their capture, it was assumed that mating had taken place in captivity some considerable time after they had moulted in the field.

The other three females moulted in captivity and spawned respectively in 9, 20 and 63 days after ecdysis. Two of them (T.C.L. 72, 79 mm) were of interest in that they spawned in spring and were consistent with Heydorn's (1966) conclusion that the smaller females are usually in berry later in the year than the larger females.

These few results suggest that the interval between ecdysis and egg-production is variable. The period of 9 to 20 days recorded in four of the females is probably more normal than the delay of 63 days observed in the fifth individual. At all events, it was noticed that most postmoult females appeared to avoid the males for several days, and it is surmised that the females are probably too weak to spawn immediately after ecdysis. Contrary to the opinions of some observers, it has been inferred that ecdysis and spawning are not necessarily closely associated in *J. lalandii*.

Retrogression of the ovaries and autolysis of the eggs have been suggested as probable causes of sterility in several species of captive decapods. Resorption

of yolk from the eggs of *Homarus americanus* has been cited by Allen (1895) and has also been reported in *Orconectes limosus* (*Cambarus affinis*) by Andrews (1906), in *Diogenes pugilator* by Bloch (1935), and in *J. lalandii* by Heydorn (1966).

It is possible that similar processes may have contributed to the negative results obtained in most of the present breeding experiments. Nevertheless, in at least three females the ovaries were large and no yolk resorption was apparent when they were examined macroscopically after an ecdysis at which long ovigerous setae were developed. As two of the females were in captivity for over a year and had survived three ecdyses, it seems that, although they did not spawn, the sexual cycle had not been markedly affected. No sections of the ovaries of these animals were prepared, and it is not known if the eggs were fully mature. Until further information on this aspect is available, a decline in the fertility of the females during long periods of captivity cannot be excluded.

From current observations, it is also doubtful if young females become mature in captivity. A few small females were maintained for two years, by which time the T.C.L. was 69 to 71 mm. Even though females smaller than this have occasionally been collected in berry, none of the young experimental females acquired ovigerous setae and the ovaries were immature. A likely explanation is that maturation of the ovaries may be delayed or inhibited by a lack of factors essential to vitellogenesis.

Another reason for the persistent sterility in most of the captive adult females may have been the approximate coincidence of their ecdyses with those of the males. As the captive males also moulted twice a year, it is feasible that they are subject to periods of sexual impotence and that, unless they moult some time before the females are furnished with ovigerous setae, mating will not take place.

When soft-bodied males were placed in tanks containing females, which had moulted and were known to have ovigerous setae, no eggs were produced. Assuming that metabolic changes correlated with moulting had affected the male sexual behaviour, it is possible that the proper stimulus for mating was lacking.

The association of freshly-collected, hard-shelled males and females, which had either recently moulted or which moulted in the presence of the males, was equally ineffectual. Although the females possessed ovigerous setae, no sexual activity was displayed.

As most of the females moulted successfully but failed to reproduce, some of them may have been either too large or too small for the available males. In one experiment, however, a female (T.C.L. 79 mm), which had moulted in isolation, spawned six days after a male (T.C.L. 100 mm) was introduced into the tank. Similarity in the size of the partners may, therefore, not be an essential attribute to successful mating, but intercourse between small males and larger females seems unlikely.

ATTEMPTS AT ARTIFICIAL INSEMINATION

When it became apparent that reproduction had failed in most of the experiments during the first half of 1966, the following four rather crude attempts were made to inseminate a number of freshly-collected mature females. All the females were soft when captured and the semen was removed directly from the vasa deferentia of mature males.

1. Spermatophoric material was smeared on the sterna behind the gonopores of three females (T.C.L. 82, 82, 83 mm).

2. Seminal substance was pressed with a spatula into the gonopores of three females (T.C.L. 75, 77, 80 mm).

The above females were captured on 26 June 1966 and were isolated for about three weeks to ensure that they had not mated recently in the field.

In the next two experiments, injection syringes with blunted fine and coarse needles were used to introduce spermatophoric matrix into the oviducts of four females. These females were isolated for nine days after their collection on 26 July 1966.

3. Pure spermatophoric material was injected into the oviducts of two females (T.C.L. 82, 84 mm).

4. As some difficulty was experienced in drawing sufficient quantities of the viscous, transparent spermatophoric mass into the syringes, a dilution of equal parts of seminal material and sea water was injected into the oviducts of two females (T.C.L. 73, 77 mm).

In each experiment the treated animals and control females of similar sizes and condition of shell were placed in separate tanks. They were observed for at least a fortnight, but none of them produced eggs.

All the females seemed to be unusually restless for several days after treatment. They moved about, either with the abdomen fully extended and with the pleopods pendent, or with the abdomen tightly flexed and simulating the ovigerous posture.

The somewhat rough handling of the specimens appeared to have no ill effect. One female, which moulted in captivity before the experiments, survived two further ecdyses. Another female moulted 36 hours after the injection of diluted seminal fluid into the oviducts and had a second ecdysis six months later. The other females had obviously moulted in the field before their capture and, although most of them were maintained for several months in tanks containing males, reproduction did not take place.

Assuming that artificial insemination would have induced spawning, one reason for the negative results could have been the time lapse between the winter ecdysis of the females and the beginning of the experiments. Nevertheless, previous comments (p. 247) show that *J. lalandii* females are capable of reproduction some time after they moult.

It has also been suggested (p. 246) that in mature females a period of sexual quiescence occurs after the breeding season and coincides with the immature condition of the ovaries and the loss of the ovigerous setae. All the females in

these experiments possessed long ovigerous setae, and it was assumed that they had not been in captivity long enough for the production of any radical changes in the state of the ovaries. Physical contact and sexual stimulation by hard-shelled males may, however, be essential to successful reproduction in this species.

Several tests indicated that the spermatophoric substance remains soft and simply disintegrates after being immersed in sea water for a few days. It is therefore probable that most of the spermatophoric material which was applied to the sterna of the first three females was washed off the surface soon after the animals were returned to the tanks.

Another factor which seemed to militate against the possible fertilization of the internal eggs of the females used in the other experiments was the rapid expulsion of the injected seminal matter through the gonopores, presumably by internal pressure either within the body cavity or in the oviducts. Thus, even if the females had been capable of reproduction at this juncture, it is doubtful if sufficient spermatophoric material was retained in the oviducts to impregnate the eggs.

No valid conclusions concerning the method of fertilization in *J. lalandii* can be drawn from these simple experiments. However, if true copulation takes place, it is still uncertain how sperm intromission is effected. It is also question-able if there is adequate provision for the storage of spermatophoric material in the oviducts. On the other hand if fertilization is external, the consistency and the rapid deterioration of the exposed contents of the vasa deferentia suggest that the eggs must be laid shortly after mating.

HISTOLOGY OF THE REPRODUCTIVE ORGANS

Histologically the gonads of both sexes of *J. lalandii* seem to be practically identical with those of *J. novaehollandiae* (Fielder, 1964*b*). In both species the testes are intricately coiled tubes and the parts of the vasa deferentia are sharply differentiated. In the present material they are divisible into three regions, the first and third of which are similar to the proximal and distal vas deferens of *J. novaehollandiae*.

The slender, convoluted proximal portion of the vas deferens (fig. 4*A*) is oval in section and its lumen is reduced to a narrow, keyhole-shaped slit by the arrangement of the columnar epithelium into small cells at the poles and elongate, very narrow cells along the two sides.

The middle and distal parts of the vas deferens are wider than the first part and each has a thick muscular wall. The slightly coiled middle region (fig. 4*B*) is lined by a villiform glandular epithelium which is produced into a conspicuous typhlosole. The latter underlies a surface streak, called the hyaline line by Matthews (1951, 1954*a*, 1954*b*), along which the wall appears to be somewhat thinner and less muscular. Some similarity is evident between sections of this region and those of the enlarged swollen part of the vas deferens
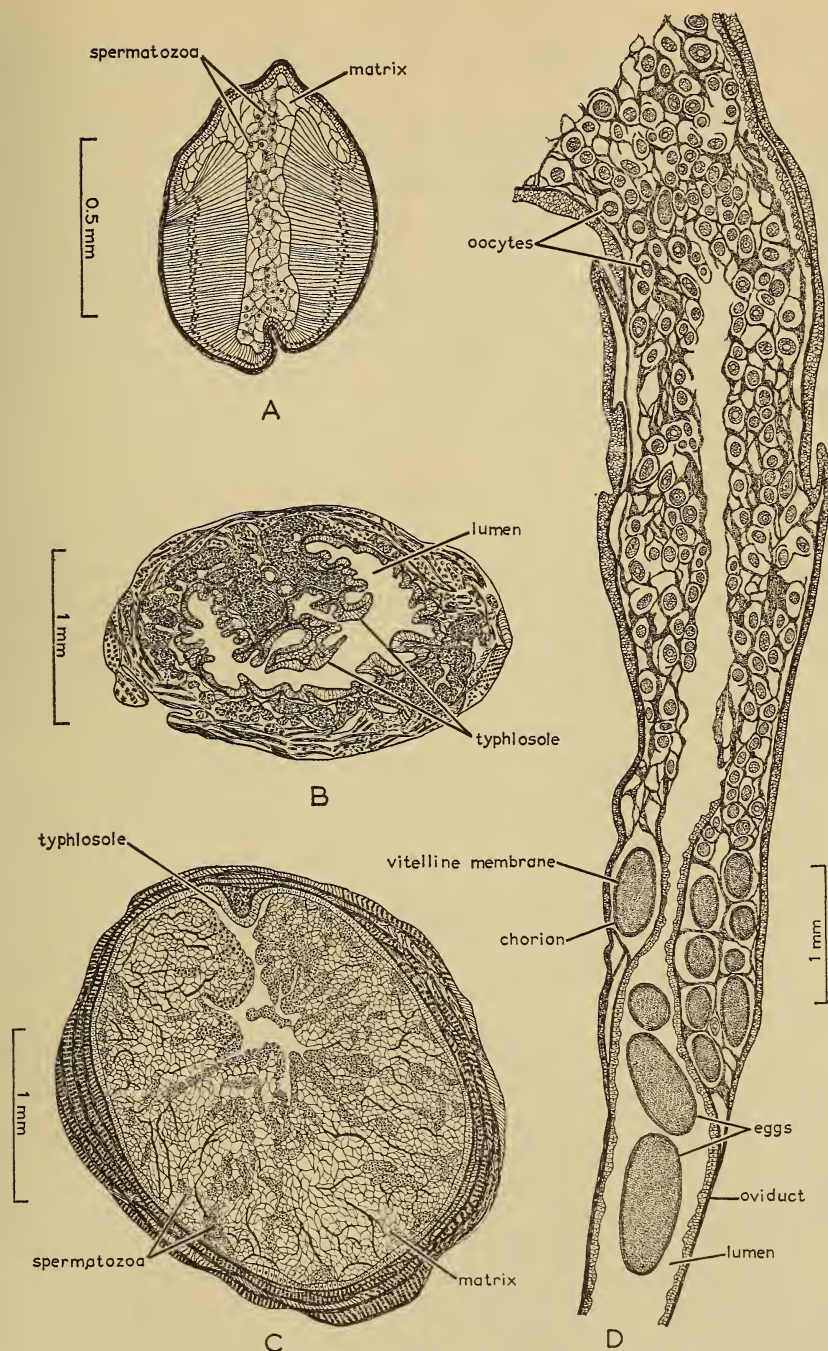
FIG. 4. Diagrammatic sections of the organs of a mature male (T.C.L. 110 mm) and an ovigerous female (T.C.L. 85 mm).
A. Transverse section through the proximal portion of the vas deferens.
B. Transverse section of the middle region of the vas deferens.
C. Transverse section of the distal part of the vas deferens.
D. Longitudinal section passing through the junction of the ovary and the oviduct.

of *Panulirus penicillatus* depicted by Matthews (1951).

The structure of the longer, straighter, and more cylindrical tube (fig. 4*C*), which passes to the gonopore, is comparable with that of the distal part of the vas deferens of *J. novaehollandiae* (Fielder, 1964*b*). The epithelium is flatter than that of the middle region, and the typhlosole is small and conical in section. The wide lumen is filled with a reticulated, folded matrix, the sinuous edges of which are charged with spermatozoa. The definite spermatophoric wall and the 'putty-like' basis of the matrix, described in *P. penicillatus* (Matthews, 1951), seem to be lacking. It is believed by Matthews (1951, 1954*a*, 1954*b*) and Fielder (1964*b*, 1964*c*) that most of the spermatophoric matrix is secreted by the typhlosole. In the present sections the matrix is absent from the middle part of the vas deferens (fig. 4*B*), but occurs in the other two regions of the duct and also in the lumen of the testis.

In sections of the testis and the vas deferens and in smears of the spermatophoric matrix of mature males the spermatozoa are small spherical bodies measuring 6·8 to 13·5 μ in diameter. As in *Palinurus elephas* (*vulgaris*) (Bloch, 1935), each spermatozoon has a distinct cupular nucleus and a globular capsule. It seems unlikely that the spermatozoa are immature but, even in thin smears, the characteristic radiating processes are indeterminate. Comparatively few spermatozoa are furnished either with one or with four to six delicate filaments measuring about 7 to 11 μ in length, and it is possible that some of these are artefacts. Heydorn (1965) has, however, detected up to five spines projecting from the spermatozoa of *J. lalandii*, and Matthews (1951) has mentioned the presence of rayed spermatozoa in *Panulirus penicillatus*.

From a number of ovigerous females examined, the one selected for microscopic study of the gonads contained mature eggs in the ovaries and the oviducts. In section, the ovary (fig. 4*D*) presents some of the features of the ovaries of *J. novaehollandiae* and *J. lalandii*, described respectively by Fielder (1964*b*) and Heydorn (1966). Numerous oocytes with a maximum diameter of 120 μ are visible. Each is enclosed in a delicate vitelline membrane and a layer of follicle cells, and in many of the oocytes the large nucleus contains a conspicuous nucleolus.

The mature eggs in the ovary and in the oviduct measure from 400 to 500 μ in diameter. In addition to the thin vitelline membrane, each is surrounded by a thicker envelope, the chorion (fig. 4*D*), which is cribriform in section. It has been shown by Herrick (1911) that the ripe eggs of *Homarus americanus* are invested by a chorion which is secreted by the egg follicle. Bloch (1935) has also suggested that, as the mature ovarian eggs of *Diogenes pugilator* are furnished with both a vitelline membrane and a chorion, the latter is not a product of the oviduct. Von Bonde's (1936) conclusion that fertilization is internal in *J. lalandii* is based on the supposition that the 'chitinous' egg membrane is secreted by the lower part of the oviduct, but his interpretation of the egg membranes may be somewhat erroneous.

The external eggs of *J. lalandii* are approximately 750 μ in diameter and

are enclosed in an additional cuticular membrane which is continuous with the egg-stalk and is believed by several authorities to be secreted by the tegumental glands of the pleopods.

Although the residual mature eggs of ovigerous females are probably destined to be resorbed, it seems logical to assume that, if intromission takes place, traces of the seminal material will remain for some time in the oviducal lumen. In the present serial sections of the oviduct, however, no spermatozoa or any substance resembling the spermatophoric matrix could be detected.

In support of Von Bonde's (1936) assumption that the eggs of *J. lalandii* are fertilized in the proximal part of the oviduct, Fielder (1964c) has proposed that the spermatozoa could be lodged in the folds of the oviducal wall after the dissolution of the spermatophoric matrix. This hypothesis has been accepted by Heydorn (1966) but has not been confirmed in the present investigation.

FERTILIZATION

Various accounts of mating and reproduction in macrurous Reptantia have shown that spermatophoric masses are deposited by the male on the sternum of a recently-moulted, soft-bodied female. It has also been suggested that in *Panulirus* the sperm are released when the female uses the chelae of the fifth pereiopods to scarify the hardened spermatophoric mass on her sternum.

In the absence of resistant external spermatophores in *J. lalandii*, it appears that the main function of the chelae is to groom the abdomen and the pleopods in both unmated and ovigerous females. Sexual dimorphism of the fifth pereiopods of this species was not apparent in small females with a T.C.L. of 26 mm. As the females increased in size, however, the process of the propodite, which forms an essential part of the chela, gradually became more pronounced.

Failure to detect the usual palinurid external spermatophores has been one of the most puzzling features in the reproductive biology of *J. lalandii*, and it has often been assumed that fertilization is internal. Microscopic examination of the reproductive organs and attempts to induce spawning by artificial insemination suggest that this supposition is unlikely.

Dissections of a number of mature females at different times of the year proved that no spermathecal enlargements occurred on the oviducts. It was also observed that, in freshly-collected, soft females possessing long ovigerous setae, the oviducts were distended with mature eggs awaiting extrusion. Moreover, the male has no intromittent organs, and no support has been found for Von Bonde's (1936) theory that the eggs are fertilized in the oviducts.

The following observation is considered to be significant in that it seems to indicate how fertilization is accomplished externally. It concerns an experiment with a female (T.C.L. 89 mm) and two hard-shelled males (T.C.L. 90, 100 mm). The smaller male had been in captivity for a month and the larger male was a recent introduction.

On 25 July 1967, 36 days after the female had moulted, she was observed in a crouched position about an hour after sunset. Mating had probably just taken place, and it appeared that spawning was imminent. The abdomen was strongly flexed and the tail-fan was fully expanded beneath the cephalothorax. An immediate examination of the female's sternum behind the gonopores revealed the presence of a fairly thick layer of colourless, gelatinous matter resembling the spermatophoric matrix.

Stained smears of some of the material, which had been kept overnight in sea water, were somewhat unsatisfactory, but the nature of the deposit was established by the identification of a number of spermatozoa. These were comparable in size to the spermatozoa observed in fixed preparations of the contents of the vasa deferentia. It was also of interest that several freshly-laid eggs were found in the vessel in which the material had been stored.

In trying to evade capture, the female had obviously been greatly disturbed at a critical period and much of the extraneous matter was dislodged in handling her. By the following morning all traces of the hyaline deposit had disappeared and, so far as is known, no more eggs were produced.

Although this isolated incident requires further confirmation, it suggests that a soft, transparent spermatophore is placed on the female's sternum during the brief act of mating. If, however, the eggs are extruded almost immediately after its application, the spermatophore will virtually be obscured. (A short report of this opinion has been submitted in a letter to the Editor of the *South African Journal of Science*, Paterson, 1969*b*.)

In several females it was observed that a considerable number of eggs were still adherent to the sternum shortly after spawning had taken place. Presumably, these eggs were embedded in the remains of the colourless, viscous spermatophoric mass. It is therefore probable that the eggs are fertilized on the female's sternum before they pass into the incubation chamber, where they become attached by stalks to bundles of the ovigerous setae on the endopodites of the pleopods.

INCUBATORY PERIOD

The period of incubation, during which the eggs are carried externally and cared for by the females, was studied in 22 specimens, 19 of which were captured in berry. As it was noted that in many of the broods some larvae emerged earlier than others, a distinction has been made between the start and the completion of hatching (table 15). The average interval between spawning and the first signs of larval eyes in the incubating eggs is also indicated.

It was observed that the incubatory period differed somewhat in individual females, but its duration may depend upon the size of the animal and on the number of eggs carried. Although no regular pattern was evident, clearance of the pleopods was generally effected sooner in some of the smaller than in the larger females in each size class.

TABLE 15

Summary of the development of the larval eyes and the length of the incubatory period in the eggs of captive females

T.C.L. in mm	No. of specimens	Development of larval eyes		Start of hatching		Completion of hatching	
		No. of days	Mean in days	No. of days	Mean in days	No. of days	Mean in days
60–69	1	32		44		81	
70–79	5	31–37		51–81		77–102	
80–89	7	29–37	32·1 ±2·6	61–81	62·2 ±11·4	78–102	94·2 ±8·4
90–99	8	28–37		51–81		85–102	
100–109	1	32		67		90	

The eyes of the developing larvae in the eggs of females which were collected in berry were apparent in 29 to 32 days. This compares with 28 to 37 days observed in the eggs of the present females which spawned in captivity. It is therefore reasonable to suppose that most of the ovigerous females had been captured shortly after the eggs were laid. On this premise, it has been concluded that the incubation of the broods was generally completed in approximately three months. Occasionally, however, the development of some embryos was retarded, and a few females moulted in spring or summer before all the larvae had hatched.

Gilchrist (1913) considered that the eggs of *J. lalandii* are carried for about five months, but in his holding experiments a shorter period of two to four months is indicated. The latter time is more consistent with an incubatory period of three to four months reported by Von Bonde & Marchand (1935).

The length of the incubatory period also appears to be variable in species of *Panulirus*. While Allen (1916) estimated that in *P. interruptus* hatching was completed in nine or ten weeks, a period of 18 days was recorded for *P. argus* by Crawford & De Smidt (1922). Contrasted with these findings, it is thought that the embryonic development lasts about a month in *P. japonicus* (Terao, 1929; Nakamura, 1940) and in *P. argus* (Sutcliffe, 1952).

DISCUSSION

Most of the important biological and ecological facts concerning *J. lalandii* have been acquired either by regular experimental trawling or tow-netting (Gilchrist, 1913, 1918; Von Bonde & Marchand, 1935; Matthews, 1962;

Lazarus, 1967) or by direct underwater observations of the animals (Heydorn, 1965, 1966). A few aquarium experiments have also been performed by some of these investigators.

The primary object of the present study was an inquiry into the mating behaviour and the process of fertilization, but several side-issues have also proved of interest. Some of these are discussed in an attempt to correlate the behavioural patterns of captive *J. lalandii* with the data obtained in the field by other workers.

Locomotor and feeding activities

As in other Decapoda, the Cape rock lobsters are more active at night than during the day, and the suggestion of a bimodal rhythm in the locomotor and feeding activities is partly substantiated by reports that the highest catches of rock lobsters are obtained by local fishermen just before daybreak.

Foraging and feeding were also observed in some captive animals during the day, and it seems unlikely that all the animals in thickly populated areas will remain strictly nocturnal in their habits. Active feeding on the sea bed has been observed during the day by Heydorn (1966), and some measure of diurnal activity also appears to be implied in the successful day-time hauls of rock lobsters described by Gilchrist (1913, 1918) and Von Bonde & Marchand (1935).

It is well known that rock lobsters are easily caught in traps or hoop nets baited with dead fish and, while the captive animals became accustomed to feeding on a daily supply of pieces of fresh stockfish, live fish and other active animals are probably not included in their normal diet.

A few small klipfish, *Clinus superciliosus* (Linnaeus), and a number of crabs, *Plagusia chabrus* (Linnaeus), lived unharmed for several months in a tank containing eight juvenile rock lobsters. It was only when the klipfish became moribund after an overnight failure of the water and air circuits that they were partly eaten by the rock lobsters. On other occasions, some klipfish and crabs were introduced into tanks containing adult rock lobsters and, although the crabs were often seen perched on the carapace of the rock lobsters, no attempts were made to attack or dislodge them.

The cardiac stomach of freshly-collected animals usually contained fragmented mollusc shells. Sometimes pieces of the exoskeleton of rock lobsters, the byssus threads and complete shell valves of small mussels, *Aulacomya magellanica* (Chemnitz), were also observed. It is therefore likely that their natural food consists mainly of sedentary organisms such as *Aulacomya*, which are said to be plentiful in rock lobster grounds. Omnivorous feeding is suggested by the preference shown by captive animals not only for lamellibranchs, but also for small limpets and kelp. They were, however, also attracted to the dead bodies and the exuviae of other rock lobsters, and cannibalism, which only occurred among crowded immature specimens, is probably resorted to when other food is scarce.

Moulting frequencies

Based on field investigations, it has been assumed that in *J. lalandii* there is an annual ecdysis which takes place in late spring or summer in the males and in late autumn or early winter in the females. Nevertheless, Gilchrist (1918) recorded the capture of a number of soft-bodied males in winter and soft females in summer. Moreover, in a study of *J. novaehollandiae*, Hickman (1945) remarked that, although most of the males moulted in spring, some catches taken during autumn and winter contained a few soft males. It is likewise pertinent that a winter ecdysis is indicated in the males of *J. tristani*, 17 of which were maintained for several months at the Sea Point Aquarium during 1967. Five of the specimens died between 15 June and 23 August just before ecdysis and, of the remaining animals, one moulted in May, five in July, three in August, and three in September.

Biannual ecdyses were common in the captive adult males and females of *J. lalandii*, and a similar frequency seems to be implied in Fielder's studies of *J. novaehollandiae*. He established (1964a) that animals with a rostrum-carapace length of 8·0 to 8·9 cm moulted twice a year. It was also noted (1964c) that four females moulted between August and October but, like most of the present specimens, they did not reproduce.

Ecdysis and spawning

As it is generally agreed that ecdysis of the females precedes spawning, the prevalence of a spring/summer ecdysis in the captive females is of interest, more particularly because in some females it was correlated with the loss of the ovigerous setae and the diminution of the ovaries. It has therefore been inferred that the annual period of sexual activity in the females is characterized by the development of long ovigerous setae and is followed by an ecdysis which marks the beginning of a period of sexual quiescence.

The presence of the ovigerous setae, either at the autumn/winter ecdysis or at the spring/summer ecdysis, suggests that two overlapping incubatory periods are possible in a given population of *J. lalandii*, one occurring from winter to spring in some females and the second from spring to summer in other females. This supposition is partly confirmed by Gilchrist's (1913) observations of captive animals and by his conclusion (1918) and that of Matthews (1962) that spawning takes place later in some areas than in others.

Two distinct breeding communities are likewise suggested by Heydorn's (1966) field observations which have shown that, while the larger females reproduce in winter, some smaller ovigerous females may still be found during the following summer. The existence of separate spawning populations has also been considered by Lazarus (1967) as a possible explanation of the occurrence of 'winter' and 'summer' hatching peaks associated with the distribution of the phyllosoma larvae of *J. lalandii*.

As embryonic development probably lasts about three months, the presence of ovigerous females throughout several seasons obviously indicates that the

females are not all fertile at the same time and that the pre-mating ecdysis of the females must likewise be staggered over five or six months.

The relatively high percentages of ovigerous females recorded in the field during spring therefore seem to be significant. They may support the theory that the population is roughly divisible into two groups, one of which spawns earlier than the other. The numbers of animals in the two groups may be disproportionate but, if the incubatory periods of some females in each sub-division happen to coincide in spring, an increase in the percentages of ovigerous females collected at that time will be expected.

The cycles of ecdyses recorded in the field do not altogether disprove this opinion, since minor peaks of ecdysis seem to be evident in spring and summer in some of the areas so far investigated. As the pre-mating ecdysis of the females is undisputed, it may be postulated that the general patterns of moulting and ovigerous females should be more equable than is apparent in most field observations, some of which hardly reflect the ecdyses of the females that spawn in spring. Moreover, the spring/summer ecdysis frequently recorded in captive unmated and post-ovigerous females has not been corroborated in the field, but it is conceivable that it corresponds to the post-incubatory ecdysis described in species of *Panulirus*.

Mating

Several investigators have indicated that in some captive Decapoda the ovaries degenerate and that reproduction is consequently suspended, yet Gilchrist (1913) demonstrated that mating recurred annually in a few experimental specimens of *J. lalandii*. In later observations, however, Gilchrist (1918) found that after a year in captivity a number of females became sterile. He tentatively suggested that spawning might occur biennially, but this seems unlikely. Most of the present females were also infertile, although post-mortem examinations of a few specimens, which had been captive for some time, showed that the ovaries looked mature and apparently had not been permanently impaired.

It has been surmised that the sexual activity of captive males was limited by their biannual ecdyses and that some were therefore unsuitable for mating with the available females. The choice of physiologically adjusted partners is doubtless a deciding factor in effective breeding experiments. When selecting hard-shelled male rock lobsters, however, it is difficult to determine whether they have already moulted in the field or whether they will moult during the reproductive period of the females.

Gilchrist (1913) gave no particulars concerning the males used in his experiments, but it is possible that the successful results were obtained by the annual introduction of new hard-shelled males. No real support for this conjecture was evident in the present study. It has been shown (p. 247) that five females produced eggs after mating with fresh hard-shelled males, but it must be noted that four of the females were also fairly recent acquisitions. The fifth

female spawned in spring after four months of captivity, but other females, which had been held for even longer periods, remained barren. It is therefore possible that reproduction in some of the females was inhibited by factors in the environmental conditions to which they were subjected.

It has usually been assumed that the annual reproductive cycle in *J. lalandii* is actuated by the ecdysis of the female and that successful mating is dependent upon the soft condition of the female. Judging by the present observations, this conclusion seems doubtful. An unusually long interval of 63 days occurred between ecdysis and spawning in one female. In four other individuals the eggs were laid in 9 to 20 days after ecdysis and while hardening of the exoskeleton was in progress.

Variations in the time between the ecdysis of the female and spawning are also evident in other reports on the biology of *J. lalandii*. An analysis of Gilchrist's (1913) experiments indicates that one female spawned on two occasions shortly after ecdysis. In other females the interval between ecdysis and mating was about 14 days and, when the time of mating was not recorded, there were periods of 38 to 47 or 48 days between ecdysis and egg-production. Matthews (1962) has also suggested that spawning probably takes place about three weeks after the females have moulted.

From these accounts, it would seem that mating in *J. lalandii* is possible when the exoskeleton has begun to harden. This conclusion is, however, at variance with the views of Von Bonde & Marchand (1935), who considered that mating and oviposition are accomplished shortly after the female has moulted. In this connexion, it is of interest that Sutcliffe (1952, 1953) has observed that in *Panulirus argus* mating may take place when both the males and the females are hard shelled.

Fertilization

Elsewhere (Paterson, 1968) it has been suggested that the male genital apparatus of *J. lalandii* resembles that of the Natal rock lobster, *Palinurus gilchristi* Stebbing. There is also a marked difference between the male gonopores of these two species and those of the east coast rock lobster, *Panulirus homarus* (Linnaeus), in an account of which firm external spermatophores have been described by Heydorn (1966).

Hard external spermatophores comparable to those of *Panulirus* have not been detected in *J. lalandii*, but some importance is attached to the discovery of a colourless gelatinous mass behind the gonopores of one of the present captive females. As this substance contained spermatozoa and resembled the transparent viscid contents of the vasa deferentia of mature males, it is believed that in *J. lalandii* a soft external spermatophore is deposited on the female's sternum. It is also anticipated that a similar external spermatophore will be found in *Palinurus gilchristi*.

The latter expectation seems to be reasonable enough, because, according to Brocchi (1875) and Bloch (1935), one investigator (Coste, 1860) reported

the presence of external spermatophores in the langouste, *Palinurus elephas* (Fabricius). In addition, some early workers were convinced that true copulation did not take place in *Palinurus* and other Macrura. It was postulated that intromission of sperm would hardly be effective in fertilizing the large number of eggs produced by each female.

A similar argument would be equally cogent in speculations regarding the method of insemination in *J. lalandii* but is no longer considered to be necessary. The present conviction that a soft external spermatophore occurs in this species confirms previous conjectures (Paterson, 1968) that fertilization is external and not internal, as has formerly been supposed. The spermatophore of *J. lalandii* apparently lacks the 'putty-like' matrix described in species of *Panulirus*, and the fact that it is transparent and transient probably explains why it has hitherto been overlooked.

Summary

Some aspects of the behaviour of juvenile females and adult males and females of the Cape rock lobster, *Jasus lalandii* (H. Milne Edwards), were studied in holding experiments at the Sea Point Aquarium, Cape Town, from March 1966 to July 1968.

Shortly after their introduction into the tanks, the animals established territorial rights to particular corners or rock niches and defended them against intruders.

Reference is made to some of the grooming operations frequently observed.

Direct observations of 18 to 20 adults over a period of four months suggested the presence of a bimodal diurnal rhythm in the locomotor and feeding activities. The normal behaviour was probably affected by the daily introduction of food during the afternoon but, even so, the levels of activity were generally higher at night than during the day.

Ecdysis, which usually took place at night, was observed in eleven juveniles and seven adults of *J. lalandii* and also in three males of *J. tristani*. An account is given of the process which is essentially similar to that described by several authors in *Panulirus*. Actual exuviation was completed in three to five minutes in *J. lalandii* and in four to seven minutes in *J. tristani*.

No significant difference was found in the average growth rates of the adult males and females, but the mean increments in the T.C.L. of the juvenile females were probably slightly higher than those of the adult females. As the animals increased in size, a progressive decrease in the growth rate was observed.

The mean moulting frequency decreased from 4·8 to 2·0 per annum as the animals became larger. Biannual ecdyses, one in autumn or winter and the other in spring or summer, occurred in the 60 to 69 mm T.C.L. size class of juvenile females and in both sexes of the adults.

A study of the ecdyses of 33 mature females revealed that the ovigerous setae were frequently developed at the autumn/winter ecdysis and were shed at

the spring/summer ecdysis. Only three of the females acquired ovigerous setae at the spring/summer ecdysis. The loss of the ovigerous setae was correlated with a diminution in the size of the ovaries.

Apparently compatible males and females were selected for breeding experiments, but most of the females failed to spawn. The coincidence of the ecdyses of the captive males and females and degeneration of the ovaries may have contributed to the persistent sterility in the adult females. Maturation of the ovaries also seemed to be delayed or inhibited in young captive females and was probably occasioned by the unnatural environmental conditions.

Mating and spawning were not observed, but four females produced eggs in 9 to 20 days after ecdysis. In a fifth female, which reproduced in spring, there was a period of 63 days between ecdysis and spawning. It has been concluded that the soft condition of the female is not necessarily a prelude to mating and egg-production.

The assumption that fertilization is internal in *J. lalandii* has not been confirmed. Attempts to inseminate several mature females gave negative results, and serial sections of the ovary and the oviduct of an ovigerous female showed no traces of spermatophoric material.

In one female, which had probably just mated and which seemed about to spawn, a transparent seminal mass, resembling the viscous contents of the vasa deferentia of mature males, was found applied to the sternum behind the gonopores. It is believed that a soft, transient spermatophoric mass occurs in *J. lalandii* and that the eggs are fertilized externally on the female's sternum shortly after mating takes place.

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APPENDIX

Summary of the incidence of ovigerous setae in captive females.

Animal No.	Aut/Wint 1966	Spr/Sum 66/67	Aut/Wint 1967	Spr/Sum 67/68	Aut/Wint 1968
5	+	−			
6	+	−			
18		+	+	−	
20		+	+		
27	+	−	+		
28	+	−			
29	+	−			
30	+	−			
31	+	−			
32	+	−			
33	+	−			
34	+	−			
35	+	−	−		
36	+	−			
37	+	−			
38	+	−			
39	+	−			
40	+	−			
46			−	−	
47			−	−	
49			+	−	
51			+	−	
55			+	−	−
57			+	−	
59				+	−
67			+	−	
68			+	−	
69			+	−	
70			+	−	
74			+	−	
75			+	−	
76			+	−	
77			+	−	